Journal of the Lepidopterists' Society
58(4), 2004, 189-195

RELATIONSHIPS AMONG POPULATION ESTIMATION TECHNIQUES: AN EXAMINATION FOR *PARNASSIUS SMINTHEUS* DOUBLEDAY (PAPILIONIDAE)

STEPHEN F. MATTER

Cincinnati Museum Center 1301 Western Ave Cincinnati OH 45203 and Department of Biological Sciences, University of Cincinnati, Cincinnati OH 45221. email: mattersf@email.uc.edu

AND

JENS ROLAND

Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9 Canada

Estimating the abundance of organisms is an important aspect of ecology. In fact, if we adhere to Krebs' (1972) definition of ecology as "the scientific study of the interactions that determine the distribution and abundance of organisms" it is fundamental to the field. Estimates of population size form the basis for ecological and conservation studies. A multitude of methodologies exist to estimate population abundance. These methods differ in their suitability for species, the assumptions involved, the accuracy of the estimates, and the effort and cost needed to perform. The most appropriate technique will likely depend on the objectives of the study and a balance between the precision and parameters needed and the cost and effort of each method. Because of differences in methodology, estimates of abundance may not be directly comparable among studies. Here, we examine the relationships among several common population estimation techniques used for butterflies.

Butterflies are popular study organisms for a variety of ecological and evolutionary questions and many species are often used as indicators in conservation studies (Blair 1999, Brown and Freitas 2000). It is our hope that this study will allow more meaningful comparisons of population data collected using different methods and provide guidance in selecting among common techniques.

Materials and Methods

Study species and site. The butterfly *Parnassius smintheus* Doubleday (Papilionidae) is abundant within subalpine meadows in the Rocky Mountains, although congeners are threatened elsewhere (Kuras et al. 2000). The butterflies' host plant, *Sedum lanceolatum* Torr. (Crassulaceae), occurs in gravelly sites above tree-line (Fownes and Roland 2002). *Parnassius smintheus* is univoltine with a flight period from mid July to September in our study area. Adults nectar on yellow flowered species such as *S. lanceolatum*, *Solidago multiradiata* (Asteraceae), and *Senecio lugens* (Asteraceae) (Matter and Roland 2002).

Transect surveys and mark-recapture of *P. smintheus* were conducted in nine meadows within a network of 21 meadows located along Jumpingpound Ridge, Alberta, Canada (51° 57'N, 114° 54'W). Each meadow was considered as containing a 'population.' Meadows are comprised of grasses, sedges, and wildflowers, and are bordered on their lower slopes by forest consisting of *Pinus contorta*, *Abies lasiocarpa*, and *Picea engelmannii*.

Population estimation methods. For transect surveys, each observer walked a path through the middle (along the longest axis) and around the circumference of a meadow tallying the number of *P. smintheus* observed at any distance in front of them. As *P. smintheus* fly more frequently when it is sunny (Ross et al., in press), observations were conducted during full sun. As a rubric, we stopped walking and counting if we could no longer see our shadow. For each survey there were between two and four observers. Transect surveys were conducted prior to mark-recapture, on the same date, to provide comparisons.

For mark-recapture estimates, we captured butterflies using hand nets and each newly captured butterfly was given a unique 3-letter code on the upper surface of each hind wing using a felt-tipped pen. For all captures, we recorded the date, time, location, and identity mark (Roland et al. 2000, Matter and Roland 2002). To equilibrate effort among populations, recapture continued until ~75% of recaptured butterflies had been previously captured that day. Populations were sampled from 3-7 times between July 27 and August 20, 2001.

Transect surveys. Transect surveys are perhaps the simplest population estimation technique. This method assumes, if multiple observers or observations are involved, a consistent path or amount of time is used, and that observers have similar ability in identification (Pollard 1977, Thomas 1983). To arrive at a population estimate for transect surveys, we calculated the mean and variance of the number of butterflies reported by the observers.

Number of individuals captured. This was the simplest mark-recapture technique. For this estimate we tallied the total number of different individuals caught during a sampling session. This and all other methods involving marked individuals (below) assume that marks are not lost, and that marking and handling do not affect behavior, survival, or the probability of capture.

Craig's Method. Craig's method is a slightly more complicated mark-recapture technique based on the frequency of capture during a single sampling session (Craig 1953, see also Southwood 1994). Thus, it uses some data often discarded by other methods, and may not be applicable for small mammals or other organisms which are usually caught only once per session or with unequal capture probability (Edwards and Eberhardt 1967, Nixon et al. 1967). Population estimation assumes that the frequency of butterflies captured once, twice, thrice, etc. follows a Poisson distribution. The number of butterflies not caught, the zero term of the distribution, is estimated and 'added' to the number of individuals caught to arrive at an estimate of population size. This method incorporates all the assumptions of marking and further assumes that all individuals in the population are at equal risk of capture at all times, i.e. there is instantaneous re-mixing upon release and no handling or marking effects that would effect capture. Craig's method also assumes that the population is closed, that is there is no birth, death, or migration during sampling. Population size was estimated using the equation:

$$\ln \hat{N} - \ln(\hat{N} - r) = s / \hat{N}$$

where $\hat{N}$ is estimated population size, r is the number of individuals captured, and s is the total number of captures (Craig's method 1, Craig 1953). We solved the equation above using the fsolve routine of Maple V. Variance of the estimate was calculated as:

$$\sigma^2_{\hat{N}} = \frac{\hat{N}}{e^{\lambda} - 1 - \lambda},$$

where $\lambda = s/\hat{N}$ (Southwood 1994). Capture probability can be estimated as $\hat{p} = r/\hat{N}$. Given $\hat{N}$ and λ, the expected number of individuals caught x times can be calculated from the Poisson equation:

$$E(\int_x) = \hat{N} e^{-\lambda} \frac{\lambda^x}{x!}.$$

Goodness of fit was evaluated by comparing these expected values to the observed values, where (observed - expected)^2/expected follows a χ^2-distribution. Evaluation can be made for each class of number of captures with one degree of freedom, or overall, by summing capture classes with degrees of freedom equal to the number of summands.

Geometric Model. Similar to Craig's method, the geometric model is also based on the frequency of capture and assumes a closed population. However the assumption of equal capture probability is modified and the model treats the number of times that an individual is captured as a geometric distribution. Population size was estimated using the equation:

$$\hat{N} = \frac{r(s-1)}{s-r},$$

and variance of the estimate as:

$$\hat{N}\hat{g} / \hat{q}^2,$$

where $\hat{q}$ = (s-r)/(s-1) and $\hat{g}$ = 1- $\hat{q}$ (Pollard 1977). Note that $\hat{g}$ is used rather than the traditional $\hat{p}$ to avoid confusion with capture probability. Capture probability can be estimated as $\hat{p} = r/\hat{N}$. Given $\hat{N}$, $\hat{q}$ and $\hat{g}$, the expected number of butterflies caught x times can be calculated as:

$$E(\int_x) = \hat{N}\hat{g}\hat{p}^x.$$

Goodness of fit can be evaluated using the same methods as for Craig's method (previous section).

Lincoln-Petersen. As opposed to the previous methods, the Lincoln-Petersen method requires captures on multiple occasions, in our case consecutive days. This method is based on the assumption that the ratio of marked individuals to the total population size will equal the proportion of marked individuals in a second sample. It assumes the assumptions for marked individuals, that populations are closed during and between sampling periods, and a constant capture probability. The equation:

$$\hat{N} = \frac{mn}{r}$$

was used to estimate population size, where m is the number of individuals marked on the first occasion, r is the number of recaptures, and n is the total number of individuals captured on the second occasion. For samples under 20, we used a small sample approximation (Baily 1952):

$$\hat{N} = \frac{m(n+1)}{r+1}$$

Variance of the estimate was calculated as:

$$\sigma^2_{\hat{N}} = \frac{m^2 n(n-r)}{r^3}$$

and as:

$$\sigma^2_{\hat{N}} = \frac{m^2(n+1)(n-r)}{(r+1)^2(r+2)}$$

for the small sample approximation (Southwood 1994). Estimated capture probability during the recapture period for the can be calculated as $\hat{p}$ = r/m (Skalski and Robson 1992).

Jolly-Seber. The Jolly-Seber method is similar to Lincoln-Petersen, but requires capture on three or more occasions. Importantly, this method relaxes the assumption of a closed population. Animals may enter the population via immigration or birth and leave the population via emigration or death. Without additional information, estimates can only be made for the combined effects of each, that is, total gain and loss to the population. The model is stochastic assuming that there is a probability that organisms will survive (not die or emigrate) from each census period to the next and that capture probability may also vary. Survival (ϕ), capture probability ($\hat{p}$), and population size ($\hat{N}$) were estimated using the program Jolly. We assumed fully parameterized models (time varying capture and survival probabilities) unless simpler models with constant survival, constant capture probability, or both constant did not significantly differ from the full model.

Analysis. We used linear regression to build predictive relationships between the population estimation methods. We constructed a separate model for each pair of methods. Because of non-linearity between some estimates, data were $\log_e$ transformed prior to analysis. Standard diagnostic techniques for regression were used including inspection of residuals and outliers. Not all population estimation techniques could be used for each sample date, e.g. sampling needed to be conducted on consecutive days for Lincoln-Petersen estimates. Thus, sample size varies among the techniques. We considered each population estimate to be an independent observation. It should be noted that some relationships involve cases where the dependent and independent variables are calculated using the same data (e.g. Lincoln-Petersen and Jolly-Seber both incorporate captures in the estimate of population size). In such cases correlations will be greater than expected by chance, affecting statistical inference; however, the regression equations describing the relationships are still valid.

Estimates for a population of known size. To estimate the accuracy of the techniques, we released a known number of male butterflies (24) into a meadow at lower altitude where they had never been observed and their host plant does not occur, but many of their nectar flowers do occur. Butterflies were released onto a nectar source at varying positions throughout the meadow. Sampling began 30 min after release. Butterflies were marked and recaptured as in the population surveys. Three observers who did not know the number of butterflies released, conducted the transect surveys and mark-recapture. We conducted one transect survey and two mark-recapture sessions separated by one hour for this population. We computed population estimates as for the natural populations. As there were only two capture sessions Jolly-Seber estimates could not be calculated.

RESULTS

There were significant, positive correlations among all the population estimation techniques (Table 1, Fig.1). Transect surveys produced the lowest estimates, while the geometric distribution provided the highest estimates of population size. Models for which a test could be preformed showed no lack of fit except for Craig's method for meadow Z.

For the population of known size (24 butterflies), the mean of the three observers' transect counts was 7.3 ± 5.3 (Var.). There were 16 and 14 captures for the first and second census, respectively. Craig's estimate for the first census was 24.4 ± 28.9 and 26.3 ± 69.5 for the second. The estimates from the geometric distribution were 40.0 ± 150.0 and 44.3 ± 304.2. The Lincoln-Petersen index estimated population size as 18.5 ± 3.5 butterflies.

DISCUSSION

The significant, positive relationships among the population estimation techniques were reassuring. Our limited investigation of the accuracy of the techniques shows that transect counts and the number of captures underestimate the actual population size. Craig's estimates were accurate while the Lincoln-Petersen estimate was lower than the actual population size, but provided a reasonable estimate. The geometric model overestimated population size. This experiment also allowed us to test our model and illustrate its utility and limitations. Note that the prediction of a single value of Y and its error for a given X in regression (prediction interval) differs from, and is greater than the distribution of Y (confidence interval) at a particular X (Zar 1999, p. 341). As an example, our transect count of

TABLE 1. Estimates of population size and associated parameters for *P. smintheus* in nine meadows along Jumpingpound Ridge. For Jolly-Seber mean values across all time periods are shown in italics if a point estimate for a particular census could not be calculated. If a model with constant capture probability or survival was uesd, mean values will be the same for all censuses and in roman text. Significant lack of fit is shown in bold. Goodness of fit is presented for the overall model for Jolly-Serber.

Meadow	Date	Transect		Captures	Craig's				Geometric				Lincoln-Petersen			Jolly-Seber				
		$\hat{N}$	$\sigma^2_{\hat{N}}$	N	$\hat{N}$	$\sigma^2_{\hat{N}}$	$\hat{p}$	χ^2	$\hat{N}$	$\sigma^2_{\hat{N}}$	$\hat{p}$	χ^2	$\hat{N}$	$\sigma^2_{\hat{N}}$	$\hat{p}$	$\hat{N}$	$\sigma^2_{\hat{N}}$	$\hat{p}$	$\hat{\phi}$	χ^2
F	8/6/01	53.5	60.5	37	88.0	466.4	0.42	0.39	158.1	2210.0	0.23	1.21	125.2	402.0	0.30	37.0	N/A	*0.42*	*0.81*	N/A
F	8/20/01	6.3	12.3	9	26.5	259.7	0.34	0.15	45.0	900.0	0.20	0.22	N/A	N/A	N/A	N/A	N/A	*0.42*	*0.81*	
G	8/6/01	66.0	882.0	75	753.6	130598.9	0.10	0.02	1462.5	527596.9	0.05	0.11	263.9	701.4	0.30	156.5	182.5	0.92	0.30	2.47
G	8/20/01	14.0	7.0	25	173.1	13484.5	0.15	0.02	325.0	50700.0	0.08	0.04	N/A	N/A	N/A	79.0	N/A	*0.66*	*0.81*	
g	8/6/01	76.5	264.5	35	329.8	50030.6	0.11	0.01	630.0	192780.0	0.06	0.19	154.2	471.3	0.25	39.0	N/A	*0.61*	*0.70*	0.01
g	8/20/01	7.0	1.0	17	28.3	48.1	0.60	0.22	47.2	233.2	0.36	0.62	N/A	N/A	N/A	N/A	N/A	*0.61*	*0.70*	
N	7/27/01	3.5	1.7	5	5.7	1.1	0.89	2.80	7.9	7.1	0.63	3.90	6.0	1.0	0.80	8.4	3.6	0.62	0.93	N/A
N	8/10/01	4.5	9.0	5	6.3	2.5	0.80	9.12	9.0	13.0	0.55	11.0	10.8	3.2	0.44	8.5	3.5	0.62	0.93	
N	8/20/01	3.0	0.0	2	3.4	6.5	0.58	0.41	4.0	8.0	0.50	0.50	N/A	N/A	N/A	3.2	2.7	0.62	0.93	
O	7/27/01	24.0	88.0	45	82.6	206.5	0.55	0.55	144.0	1013.8	0.31	2.33	65.5	71.7	0.70	46.0	N/A	0.67	0.91	3.77
O	8/10/01	36.0	123.3	87	110.5	44.2	0.79	12.89	176.1	364.8	0.49	4.08	196.8	579.4	0.45	271.1	N/A	0.67	0.94	
O	8/20/01	18.0	98.0	31	69.7	341.5	0.45	4.69	124.0	1488.0	0.25	2.81	N/A	N/A	N/A	N/A	N/A	0.67	0.94	
R	8/2/01	1.3	0.9	3	6.6	29.0	0.46	0.18	9.0	54.0	0.33	0.18	10.0	16.7	0.20	5.0	N/A	*0.67*	0.20	N/A
R	8/16/01	6.0	0.0	14	24.0	45.6	0.58	0.43	40.0	212.3	0.35	1.18	42.0	147.0	0.43	14.0	N/A	*0.67*	*0.62*	
S	8/2/01	12.0	38.7	18	27.8	38.9	0.65	0.74	45.8	180.2	0.39	1.29	36.0	54.0	0.56	88.6	24.5	0.84	0.65	0.02
S	8/16/01	2.7	0.3	16	25.8	41.3	0.62	1.63	42.7	189.6	0.38	3.33	43.2	181.4	0.22	32.0	N/A	*0.92*	*0.77*	
Y	8/14/01	4.3	4.3	14	18.6	11.2	0.75	5.32	29.2	65.8	0.48	3.36	23.3	31.1	0.36	14.0	N/A	1.00	0.83	N/A
Z	8/14/01	93.3	212.3	156	252.3	378.5	0.62	**11.83**	433.9	2150.5	0.36	7.96	309.7	700.1	0.44	179.3	1040.1	0.78	0.82	3.38

7.3 results in predictions of 26.0 ± 4.6 (95% P.I.) for Craig's estimate, 12.9 ± 3.5 for the number of captures, and 32.5 ± 3.9 for the Lincoln-Petersen estimate. The actual estimates fall within the prediction intervals for Craig's estimate and the number of captures, but not for the Lincoln-Petersen method. This demonstration illustrates both the utility of our model and its difficulties. For small population sizes it may be difficult to obtain a precise estimate. This problem can especially be seen by the fact that the intercepts of some relationships were significantly different from zero (Table 2). For example, a transect count of zero may indeed indicate the presence of no butterflies, but could result in an estimate of 6.6 based on the Lincoln-Petersen estimate.

Although the equations presented here apply only to *P. smintheus* at our study site, the results do illustrate the relative strengths and weaknesses of the various techniques. Given the varying reasons for estimating population abundance, a variety of methods have been and will continue to be used. For butterflies, transect surveys are perhaps the easiest and least disruptive method of population estimation requiring only the ability to identify species on the wing. For some groups or assemblages this may be quite difficult, necessitating either netting or grouping of species that cannot be distinguished. For conspicuous, easily identifiable, species transect surveys are an efficient means to generate relative estimates provided observability (capture probability in mark-recapture terminology) does not vary. However, transect surveys do not provide accurate estimates of population size, nor do they allow for estimation of observability which limits their utility for comparison. Transect surveys, as conducted here under highly favorable conditions, result in large underestimates of population size. This underestimation is especially important in determining presence or absence. A transect survey producing no butterflies does not mean that the species is absent. Accurate determination of local absence or extinction always will require additional, intensive sampling.

All other methods investigated here require both the capture and marking of individuals which may alter behavior (Mallet 1987). In general, capture temporarily reduces the propensity of butterflies to fly. Reduced flight in turn lowers the capture probability of marked individuals relative to unmarked individuals for the length of time that the butterflies are affected (Gall 1985). Frequency of capture methods (Craig's and geometric) will be more influenced by a temporary change in behavior than other methods. If marked individuals temporarily have a lower capture probability than unmarked individuals, estimates of population size will be higher than the actual population size (Gall 1985). For other mark-recapture methods, any temporary handling effect usually will have abated by the next census period. For *P. smintheus* the effects of marking on flight are minimal; however capture probability is lower for females than for males violating the assumption of equal capture probability for Craig's and the Lincoln-Petersen methods (Roland et al. 2000, Matter and Roland 2002). We note that our estimates for a population of known size used only males, and thus should not violate this assumption; however, this bias will affect estimates for the populations along Jumpingpound Ridge.

The number of individuals captured underestimates population size as the capture rate rarely nears 100 percent. However, assuming marks are not lost, the number of individuals captured does provide an estimate of the minimum possible population size. For the effort of tallying the number of times each individual butterfly is captured, Craig's method provides fairly accurate estimates of population size at a specific time, while the geometric distribution overestimated population size. Interestingly, both frequency of capture methods showed good fits to the data despite assuming different distributions for capture frequency. In general, fits were better for Craig's method than for the geometric distribution. This result contrasts with Pollard (1977) who found better fits for the geometric distribution than for the Poisson distribution of Craig's method in his investigation of three butterfly species. Our result is all the more surprising given that the geometric distribution should better accommodate the difference in capture probability between males and females than should the Poisson distribution.

The Lincoln-Petersen method requires capture on two or more, and Jolly-Seber on three or more occasions. Both provide good population estimates provided assumptions are met (Southwood 1994). In our study, it is unlikely that we meet either the assumptions of a closed population or equal capture probability required by the Lincoln-Peterson method. For the Lincoln Peterson method, the loss and gain of individuals after the initial marking period will result in overestimation of population size (Gall 1985). Jolly-Seber has the advantage of providing parameters for capture, survival, and recruitment, but requires more sampling occasions.

ACKNOWLEDGEMENTS

We thank R. Cormier, E. Robinson, A. Ross, D. Roth, C. Schmidt, and D. Sjostrom for assisting with the mark-recapture and E. Connor, C. Penz, and two anonymous reviewers for comments and suggestions improving the manuscript. This research was supported by NSF grant 03-26957 and an NSERC operating grant.

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Received for publication 8 Setember 2003; revised and accepted for publication 3 February 2004

TABLE 2. The relationship among population estimation methods. The dependent variable is in columns and the independent variable is in rows. The regression equation (SE) is on top and statistics for the relationship in the bottom of each cell. All relationships were significant ($P < 0.001$). A ** indicates that the intercept differs significantly from 0 ($P < 0.05$).

	Transect	Craig's	Geometric	Number of captures	Lincoln-Petersen	Jolly-Seber
Transect		1.17±0.36** 1.05±0.13 R^2=0.80 $F_{1,16}$=64.2	1.48±0.40 1.12±1.45 R^2=0.79 $F_{1,16}$=59.7	0.97±0.29** 0.80±0.11 R^2=0.78 $F_{1,16}$=57.3	1.89±0.34** 0.80±0.12 R^2=0.81 $F_{1,11}$=46.41	1.54±0.46** 0.77±0.16 R^2=0.64 $F_{1,13}$=22.7
Craig's	-0.41±0.32 0.77±0.10 R^2=0.80 $F_{1,16}$=64.2		0.20±0.04** 1.08±0.01 R^2=0.99 $F_{1,16}$=1093.2	0.31±0.33 0.70±0.08 R^2=0.82 $F_{1,16}$=73.5	0.95±0.30** 0.79±0.07 R^2=0.91 $F_{1,11}$=113.5	0.83±0.48 0.70±0.12 R^2=0.73 $F_{1,13}$=35.2
Geometric		-0.18±0.40** 0.93±0.01 R^2=0.99 $F_{1,16}$=1093.2		0.19±0.34 0.65±0.08 R^2=0.82 $F_{1,16}$=72.0	0.78±0.32** 0.74±0.07 R^2=0.91 $F_{1,11}$=112.3	0.72±0.50 0.65±0.11 R^2=0.73 $F_{1,13}$=34.6
Number of captures	-0.41±0.41 0.98±0.13 R^2=0.78 $F_{1,16}$=57.3	0.30±0.43 1.17±0.14 R^2=0.82 $F_{1,16}$=73.5	0.53±0.47 1.26±0.15 R^2=0.82 $F_{1,16}$=72.0		0.74±0.31 1.04±0.10 R^2=0.92 $F_{1,11}$=118.7	0.52±0.34 1.00±0.11 R^2=0.87 $F_{1,13}$=85.8
Lincoln-Petersen	-1.42±0.62** 1.01±0.15 R^2=0.81 $F_{1,11}$=46.4	-0.77±0.45 1.16±0.11 R^2=0.91 $F_{1,11}$=113.5	-0.58±0.48 1.24±0.12 R^2=0.91 $F_{1,11}$=112.3	-0.39±0.33 0.88±0.08 R^2=0.92 $F_{1,11}$=118.7		0.16±0.60 0.86±0.14 R^2=0.76 $F_{1,11}$=35.5
Jolly-Seber	-0.37±0.64 0.83±0.17 R^2=0.64 $F_{1,13}$=22.7	0.14±0.65 1.05±0.18 R^2=0.73 $F_{1,13}$=35.2	0.34±0.70 1.13±0.19 R^2=0.73 $F_{1,13}$=34.6	-0.07±0.34 0.87±0.09 R^2=0.87 $F_{1,13}$=85.8	0.80±0.56 0.89±0.15 R^2=0.76 $F_{1,11}$=35.5	

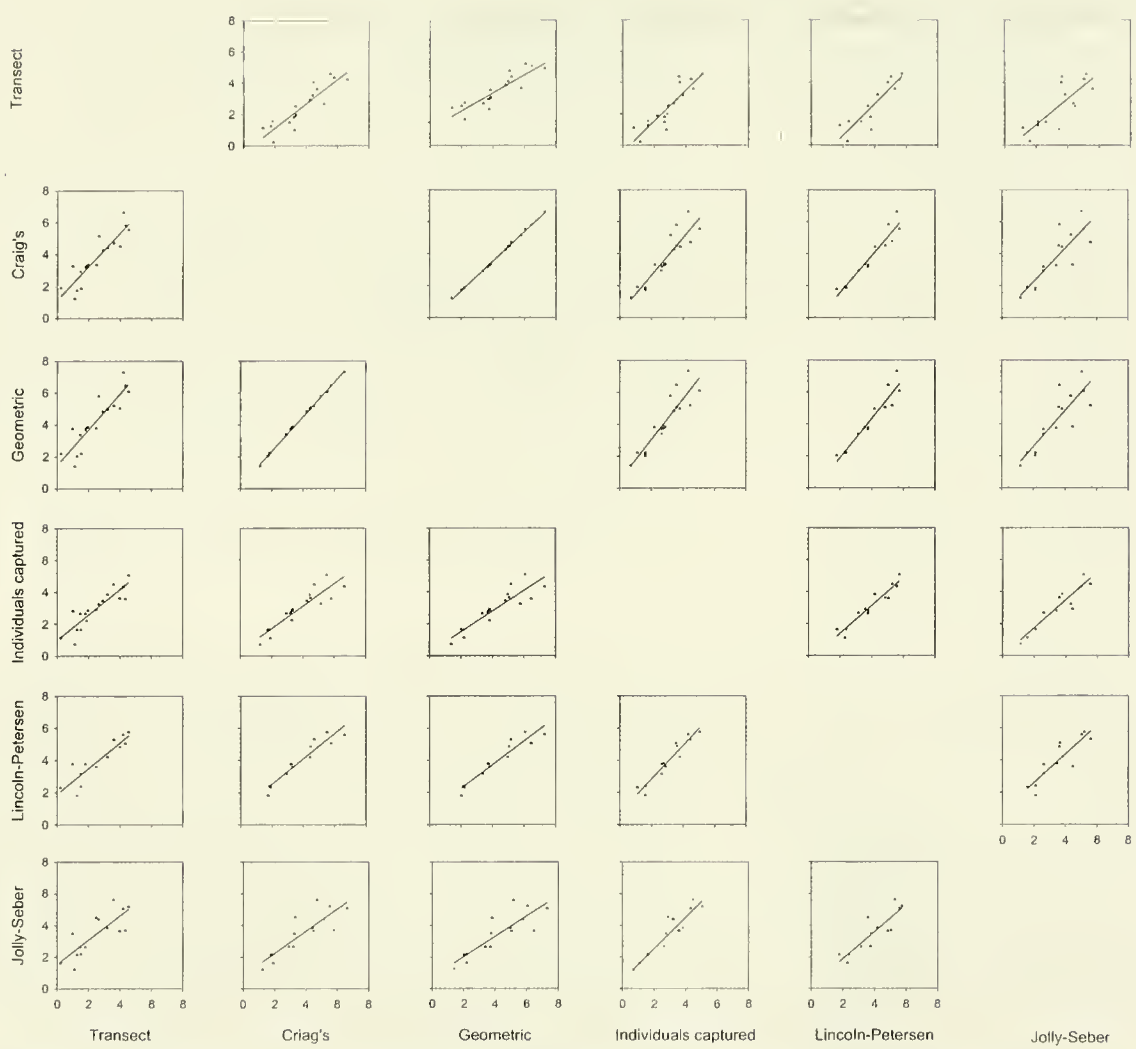

FIG. 1. Relationships among population estimation methods. Population sizes of the butterfly *Parnssisus smintheus* were estimated from 3-7 times in nine meadows using several population estimation techniques. The realtionship between each pair of techniques was evaluated using linear regression. Data were $\log_e$ transformed prior to analysis.